

Photosynthate partitioning and nodule formation in soybean plants that received red or far-red light at the end of the photosynthetic period

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Kasperbauer, M. J., Hunt, P. G. and Sojka, R. E. 1984. Photosynthate partitioning and nodule formation in soybean plants that received red or far-red light at the end of the photosynthetic period. – *Physiol. Plant.* 61: 549–554.

The influence of row orientation on spectral distribution of light received by growing soybean [*Glycine max* (L.) Merr. (cv. Coker 338)] plants was measured under field conditions, and light spectrum effects on photosynthate partitioning were studied under controlled environments. Light received by leaves under field conditions differed among those grown in north-south vs east-west oriented rows. In morning and late afternoon, the far-red/ red ratio received by leaves at the surface of the canopy differed about 3-fold from the east to west sides of north-south rows, but only 1.3-fold from the south to north sides of east-west rows.

In controlled environments, brief exposures to red or far-red light at the end of the photosynthetic period influenced partitioning of photosynthate among leaves, stems and roots. The top/root ratios differed significantly between the red and far-red treated plants. Red treated plants partitioned less photosynthate to stems and more to roots than did those treated with far-red. Also, plants with larger root systems developed more nodules. Phytochrome effects on photosynthate partitioning between tops and roots may influence yield of soybean plants grown in soils with low water-holding capacity.

Additional key words – *Glycine max*, phytochrome, plant adaptation, plant bio-regulation.

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Introduction

A better understanding of fundamental physiological phenomena should aid development of crop management systems that increase yield and quality of crop plants without increasing expenditure of natural resources. Recently, it was observed that soybean [*Glycine max* (L.) Merr.] seed yield was interactive with row orientation, irrigation and the strain of *Rhizobium japonicum* under field conditions on soil with low water-holding capacity (Hunt et al. 1982, Sojka et al. 1980). The yield difference might have been associated with soil temperatures (Munevar and Wollum 1982), which varied with row orientation and moisture content of the

soil (Hunt et al. 1982). Another possible explanation is that differences in light quality (spectral balance) might be associated with row orientation, and the light quality differences might influence growth and developmental patterns such as the top/root ratio.

Work with tobacco (*Nicotiana tabacum* L.) has shown that light quality during plant development influences the photosynthetic system (Kasperbauer and Hamilton 1984, Kasperbauer and Peaslee 1973) and the partitioning of photosynthate among leaves, stems and roots (Kasperbauer 1971). A few minutes of red light at the end of the daily photosynthetic period puts phytochrome in the far-red-absorbing form and results in plants with relatively large thick leaves, short stems and

Received 13 December, 1983; revised 15 March, 1984

large root mass. Conversely, a few minutes of far-red light at the end of the daily photosynthetic period results in thinner leaves, taller and heavier stalks and a smaller root system. Under field conditions, tobacco plants from crowded populations resembled those that received end-of-day far-red under controlled environments.

We hypothesized that the soybean yield differences associated with row orientation may be related to differences in spectral distribution of light because of shading and reflection patterns, especially near the end of day. Also, the amount of photosynthate translocated to the roots may influence the symbiotic relationship with *Rhizobium japonicum* and plant performance under moisture stress conditions.

The objectives of the present study were to (a) measure the far-red to red ratios in north-south vs east-west rows, and (b) study effects of red and far-red light at the end of the photosynthetic period on morphological development and nodule formation in soybean plants grown under controlled environments in which temperature and total light energy were held constant.

Materials and methods

Field

Soybean [*Glycine max* (L.) Merr. cv. Coker 338] plants were used in field and controlled-environment studies.

Field plants were about 4 cm apart in rows that were 75 cm apart in irrigated plots at the Coastal Plains Soil and Water Conservation Research Center, Florence, South Carolina. Rows were oriented either north-south or east-west. There were four replicates. Spectral distributions of light that reached leaves at the surface of the canopies were measured with a LiCor Spectroradiometer LI-1800 with a remote cosine receptor on a fiber optic probe when the plants were in early-bloom stage. Spectral distribution of radiation at 5 nm intervals between 300 and 850 nm received by leaves near the top of the canopy was measured parallel to the soil and at a 45° angle from the soil. A reference spectrum was obtained by measuring direct radiation above the plant canopy. Spectral irradiances at 735 and 650 nm were used to calculate the far-red/red photon fluence rate ratios. These values were used because they approach the peaks for phytochrome action spectra in green plants; 650 nm was used instead of 660 nm because chlorophyll competition for light at 660 nm shifts the phytochrome action peak to about 650 nm (Kasperbauer et al. 1963).

Controlled environment

Seedlings were started and grown in a commercial potting soil mixture (Pro-Mix BX) with high organic content or in a vermiculite:potting soil mixture under a controlled environment in which all plants received the same temperature and total light energy. Treatment

variables were the soil medium, not inoculated or inoculated with *Rhizobium japonicum*, and brief irradiation with red or far-red light at the end of the photosynthetic period each day to put phytochrome predominantly in the far-red absorbing or the red absorbing form, respectively, at that time.

Seeds were washed for 15 s in 95% ethyl alcohol and rinsed in sterile water to minimize surface contaminants. The vermiculite was washed overnight in pH 5 acidified water. Fine particles settled out and were discarded. The potting soil was used in one series and a mixture of vermiculite and potting soil (3:1, v/v) was used in the other. Three l of medium were used in each pot. Five seeds were sown per pot. Seeds in one-half of the pots of each soil medium were inoculated with *R. japonicum* strain 1004. Seeds were germinated at 28°C. After emergence, the seedlings were thinned to two per pot. All pots were watered with half-strength Hoagland's nutrient solution (Hoagland and Arnon 1950), without nitrogen twice per week throughout the experiment.

All plants were grown in the same controlled-environment chamber at 25°C with 12-h days of cool-white fluorescent light at 65 W m⁻² between 400 and 700 nm. At the end of the daily light period, plants were exposed to either 5 min of red (3.6 W m⁻² in the 600 to 700 nm waveband) or 5 min of far-red (3.6 W m⁻² in the 700 to 770 nm waveband) light at 25°C, then returned in darkness to the growth chamber for the remainder of the 12-h night. Another set received 5 min far-red followed immediately by 5 min of red light. The red and far-red treatments began when seedlings reached the unifoliate leaf stage and were repeated each day for 21 days. At the end of the 12-h dark period following the last red and far-red treatments, plants were harvested, divided into leaf blades, stems and petioles, roots and nodules. Nodules were counted and the plant parts weighed (fresh), frozen, freeze-dried, and weighed to obtain dry weights. The two plants in each pot were pooled, constituting a replicate. There were 3 replicates of each of 12 treatments (i.e. red vs far-red vs far-red followed by red, + or - inoculum, and high or low N in the soil medium).

Results and discussion

Field

Differences in the far-red/red ratio at the outer surface of soybean plants in north-south vs east-west oriented rows are shown in Tab. 1. Light measurements were taken at the upper part of the plant because that portion was still growing and, as such, could display growth responses to phytochrome manipulation (Kasperbauer and Hamilton 1984, Schäfer 1981). The far-red/red ratio parallel to the soil surface on the east side of north-south rows was similar to that of the direct sunlight control and about one-third as high as that on the west

Tab. 1. Far-red/red photon fluence rate ratios at the outer surface of the upper canopy of soybean plants grown in north-south (N-S) or east-west (E-W) rows. Spectral measurements were taken from 0852 to 0944 h on 27 July 1983 near Florence, SC. The sky was partly overcast and the far-red/red photon fluence rate ratio above the canopy was 1.05. Values followed by the same letter do not differ significantly at $P = 0.05$.

Row orientation	Side of row	Far-red/red photon fluence rate ratio	
		Parallel to soil	45° angle from soil
N-S	East	1.13 d	1.72 d
	West	3.29 c	6.14 a
E-W	North	1.51 d	3.10 c
	South	1.90 d	4.84 b

side of the same rows. At the time of measurement, the sun was in the east, and the ratio difference was due to greater amounts of far-red light being reflected back from the east side of the adjacent row. Ratios taken at 45° from soil level followed the same pattern as those parallel to the soil, but the values were higher because of relatively more far-red reflection from the numerous lower leaves in adjacent rows. The far-red/red ratio of light reflected upward from adjacent plants might be an important factor in causing leaf orientation differences between plants grown in sparse and dense populations.

Light measurements taken in late afternoon (values not shown) were similar in magnitude to those taken in the morning for the east and west sides of the north-south rows; however, the relative values were reversed because of the diurnal change in solar position. The important point to consider in these observations is that there were differences in the spectral distribution of light received by soybean plants growing in north-south vs east-west rows. Thus, it is possible that light spectrum as well as temperature differences may have accounted for growth and yield differences associated with soybean row orientation as observed by Hunt et al. (1982).

Controlled environments

The controlled environment experiment allowed evaluation of light quality effects while keeping temperature and total irradiance constant. Stem elongation and dry matter partitioning were studied.

Stem elongation. Under field conditions, plants grown in crowded populations develop long internodes and few lateral branches, while isolated plants of the same species often develop short, thick stems and numerous lateral branches. Thus, the plants must contain some sensing mechanism that determines the amount of competition and directs plant development to favor survival under what is detected as the prevailing environment (Holmes and Smith 1977, Kasperbauer 1971, Smith and

Tab. 2. Internode lengths of soybean plants that received 5 min irradiations with red, far-red, or far-red followed immediately by red light at the end of 12 h photosynthetic periods for 21 consecutive days. Values are means in mm for 24 plants. Those within the same line followed by the same letter do not differ significantly at $P = 0.01$.

Internode	Irradiation		
	Red	Far-red	Far-red + Red
Second	32 b	65 a	29 b
Fourth	56 b	116 a	56 b

Holmes 1977). Row orientation (Tab. 1) and plant spacing modify the far-red/red ratio of light received by leaves, and this may influence partitioning of photosynthate among plant organs for better adaptation. In the present experiment, effects of red and far-red light at the end of the daily photosynthetic period on stem elongation were evident in less than a week and became more pronounced as the treatments continued. Internodes of plants that received far-red light last each day elongated much more than those of plants that received red light last each day (Tab. 2). The pattern continued throughout the experiment, and effects of a brief exposure to far-red were negated when the far-red was followed immediately by a brief exposure to red light. The red and far-red reversible response implies involve-



Fig. 1. Soybean plants grown under 12-h photosynthetic periods that ended with 5 min red (left) or 5 min far-red light (right) each day for 20 consecutive days.

ment of phytochrome in the environment-sensing mechanism (Borthwick 1972). Our results with soybean are consistent with those reported for tobacco as discussed above and for pinto bean (*Phaseolus vulgaris* L.) (Downs et al. 1957).

Representative plants were photographed after 20 consecutive days of treatment (Fig. 1). Plants that received the far-red treatment began flowering a few days later than those that received red light last each day. This response was consistent with earlier observations (M. J. Kasperbauer and H. A. Borthwick, unpublished) with two short day species, *Chenopodium rubrum* L. and *Nicotiana tabacum* L. Far-red immediately after an 8-h photosynthetic period greatly delayed flowering in those species. Far-red after a 12-h photoperiod also delayed flowering, but to a lesser degree.

Axillary branching. After 20 days of treatment, soybean plants that received red light last each day had developed some axillary branches, while the far-red treated plants did not develop any (Fig. 1). The implica-

tion is that the relative amount of far-red or red light, acting through the phytochrome system, signaled the plant to partition photosynthate among organs for better survival. That is, to elongate stems after a high ratio of far-red/red signaled that there was competition from other plants, or to partition less to stems and more to axillary branches and leaves when a predominance of red light signaled that there were no competing plants. This phenomenon helps to explain why, under field conditions, plants of many species branch profusely or remain relatively unbranched depending upon the plant population density.

Partitioning. Distribution of dry matter among plant components is summarized in Tabs 3, 4 and 5. Although there were differences among plants grown in the organic potting soil vs those grown in vermiculite, the red-treated plants partitioned less dry matter to stems and more to roots relative to the far-red treated plants within each potting medium. Also, inoculated plants developed more nodules under the red light treatment.

Tab. 3. Effects of light quality, inoculant and soil medium on dry matter partitioning in soybean plants.

Treatments		Top growth		Root growth		Top/ root ratio	Nodules per plant	Leaf mass/ area
Light	Inoculant	Leaf blades	Stems + petioles	Roots	Nodules			
		mg DW (plant) ⁻¹				Ratio	No.	mg DW cm ⁻²
<i>Potting soil</i>								
Red	+	1338	533	443	4.4	4.20	4.2	2.57
	—	1548	646	462	—	4.78	—	2.61
Far-red	+	1310	836	355	1.5	5.99	2.0	2.38
	—	1127	745	300	—	6.24	—	2.35
<i>Vermiculite</i>								
Red	+	1224	653	758	134.0	2.13	100.8	2.21
	—	1165	628	876	—	2.05	—	2.63
Far-red	+	1370	1034	534	119.5	3.69	59.3	2.19
	—	1300	1001	771	—	2.98	—	2.50

Tab. 4. Percentages of dry matter partitioned to leaves, stems, roots and nodules during a 21-day period. Values are percentages.

Treatment		Top growth			Root growth		
Light	Inoculant	Leaf blades	Stems + petioles	(Total)	Roots	Nodules	(Total)
<i>Potting Soil</i>							
Red	+	57.7	23.0	(80.7)	19.1	0.2	(19.3)
	-	58.3	24.3	(82.6)	17.4	-	(17.4)
Far-red	+	52.3	33.4	(85.7)	14.2	0.1	(14.3)
	-	51.9	34.3	(86.2)	13.8	-	(13.8)
<i>Vermiculite</i>							
Red	+	44.2	23.6	(67.8)	27.4	4.8	(32.2)
	-	43.6	23.5	(67.1)	32.8	-	(32.8)
Far-red	+	44.8	33.8	(78.6)	17.4	3.9	(21.3)
	-	42.3	32.6	(74.9)	25.1	-	(25.1)

Tab. 5. Summary of statistical differences for partitioned dry matter in soybean plants grown under the various environmental treatments shown in Tab. 3. * and **, statistical significance at $P = 0.05$ and $P = 0.01$, respectively, and NS, not significant at $P = 0.05$.

Source of variation	Top growth		Root growth		Top/root ratio	Leaf mass/area
	Leaf blades	Stems + petioles	Roots	Nodules		
Light (L)	NS	**	**	*	**	**
Media (M)	NS	**	**	**	**	*
Inoculation (I)	NS	NS	NS	**	NS	**
L \times M	*	NS	**	*	NS	NS
L \times I	NS	NS	NS	*	NS	NS
M \times I	NS	NS	NS	**	**	**
L \times M \times I	NS	NS	NS	*	NS	NS

As a consequence of this pattern of partitioning among organs, the ratio of dry matter above ground to that below ground was considerably higher for the far-red treated plants within each medium. The relative amount of photosynthate partitioned to the root system may be an important factor for plant survival and productivity under moisture stress conditions in soils with low water-holding capacity. Also, differences might be accentuated or diminished by direct affect of the symbiotic relationship with *R. japonicum* or by indirect feedback regulation from the *R. japonicum*.

The trends observed in our experiments support the concept that the phytochrome system within the plant senses the amount of competition for light by other plants and initiates events leading to the partitioning of its photosynthate. The partitioning generally results in adaptation for better survival under the perceived conditions. Chlorophyll in the competing leaves absorbs much blue and red light while transmitting and/or reflecting most of the far-red light (Holmes 1981, Kasperbauer 1971, Moss and Loomis 1952). As a consequence, an individual plant receives relatively more or less reflected far-red light, depending on the number and size of competing plants and/or row orientation in the case of row crops such as soybean (Tab. 1).

Our data support the hypothesis that light quality influences partitioning of photosynthate to modify stem elongation, root development, and, perhaps indirectly, nodulation. We visualize that phytochrome is involved in the environment-sensing mechanism in the plant and that it initiates events that modify the balance of endogenous growth regulators, which function in adaptation of the plant to better survive in its growth environment. For example, red radiation has been shown to decrease assayable auxin (Fletcher and Salik 1964, Lockart 1964). Exogenous gibberellin counteracted the stem growth inhibitory effects of red light. Lockhart (1964) and other investigators (Sachs and Thimann 1964) showed that lateral buds could be released from apical dominance by application of cytokinins to topgrowth of plants. Also, it is known that synergisms and antago-

nisms exist between growth regulator groups, and relative concentration changes can influence growth patterns (Letham 1967). It appears that the partitioning of photosynthate among leaves, stems, and roots (Tab. 3) was controlled by a shift in the endogenous growth regulator balance as a consequence of the relative far-red/red ratio, especially at the end of the daily photosynthetic period or, conversely, at the beginning of the 12-h uninterrupted night following the photosynthetic period. Further work on the physiological phenomena influenced by factors such as the far-red/red ratio associated with row orientation and plant population should provide a better basis for *bioregulation* of plant developmental processes.

Acknowledgements – We thank Dr A. G. Wollum II for the isolate of *R. japonicum* strain 1004. Mention of trademark, proprietary product, or vendor anywhere in this paper does not constitute a guarantee or warranty of the product by the U.S. Dept of Agriculture or the South Carolina Agricultural Experiment Station and does not imply its approval to the exclusion of other products or vendors that may also be suitable.

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